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ORIGINAL PAPER

Feeding behavior of the ctenophore *Thalassocalyce inconstans*: revision of anatomy of the order Thalassocalycida

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Abstract Behavioral observations using a remotely operated vehicle (ROV) in the Gulf of California in March, 2003, provided insights into the vertical distribution, feeding and anatomy of the rare and delicate ctenophore *Thalassocalyce inconstans*. Additional archived ROV video records from the Monterey Bay Aquarium Research Institute of 288 sightings of *T. inconstans* and 2,437 individual observations of euphausiids in the Gulf of California and Monterey Canyon between 1989 and 2005 were examined to determine ctenophore and euphausiid prey depth distributions with respect to temperature and dissolved oxygen concentration [dO]. In the Gulf of California most ctenophores (96.9%) were above 350 m, the top of the oxygen minimum layer. In Monterey Canyon the ctenophores were more widely distributed throughout the water column, including the hypoxic zone, to depths as great as 3,500 m. Computer-aided behavioral analysis of two video records of the capture of euphausiids by *T. inconstans* showed that the ctenophore contracted its bell almost instantly (0.5 s), transforming its flattened, hemispherical resting shape into a closed bi-lobed globe in which seawater and prey were engulfed. Euphausiids entrapped within the globe displayed a previously undescribed escape response for krill ('probing behavior'), in which they hovered and gently probed the inner surfaces of the globe with antennae without stimulating further contraction by the ctenophore. Such rapid bell contraction could be effected only by a peripheral sphincter muscle even though the presence of circumferential ring musculature was unknown for the Phylum Ctenophora. Thereafter, several live *T. inconstans* were collected by hand off Barbados and microscopic observations confirmed that assumption.

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Introduction

Ctenophores are exceptionally fragile, easily fragmented by nets and trawls, but knowledge of the phylum has increased greatly due to individual collection of undamaged specimens in containers by scuba divers, submersibles and remotely operated vehicles (ROVs) (Swanberg 1974; Hamner 1975; Hamner et al. 1975; Harbison et al. 1978; Madin 1990; Robison 1999; Youngbluth and Båmstedt 2001; Gasca and Haddock 2004). Further, submersibles and ROVs collect and record video below scuba diving depths, essential for behavioral research on midwater and deep-sea animals (Hamner 1985).

Thalassocalyce inconstans is a particularly delicate ctenophore, with thin, flaccid tissues; it is the sole member of the order Thalassocalycida (Madin and Harbison 1978). No new information on this ctenophore has been published since the original description, although it had been assumed to be a cosmopolitan midwater species. The Monterey Bay

Aquarium Research Institute (MBARI) has been using ROVs since 1988 for midwater research to depths of 4,000 m (Robison et al. 2003, 2005b), and its library of archived observations can be searched for relevant information. New observations from scuba divers, the MBARI ROVs, and from archived information from ROV records have provided us with new insights about the behavior and anatomy of *T. inconstans*.

Comprehensive data sets and annotated video footage are invaluable for investigations of rare and delicate species like *T. inconstans* (Madin and Harbison 1978). *T. inconstans* has no tentacles hanging outside the bell, nor does it have muscular, thickened lobes with which to capture food (Fig. 1). It was first described as having a hemispherical medusoid shape when fully expanded but a bi-radial shape when partially contracted into a "two-globe form" (Fig. 1b) (Madin and Harbison 1978). It apparently feeds by relatively slow contraction of its medusa-like "bell," catching small crustaceans on the mucus-covered inner surface of the thin and flaccid bell, which, despite substantial differences in morphology, "functions analogously to the oral lobes" in many lobate ctenophore species (Harbison et al. 1978; Madin and Harbison 1978).

This paper is in three parts: (1) analysis of 288 behavioral and distributional records of *T. inconstans* from the MBARI archives, (2) analysis of a long video sequence recorded from an ROV in the Gulf of California showing *T. inconstans* feeding and the escape behavior of a trapped euphausiid, as well as a shorter, similar video sequence from Monterey Canyon, both analyzed via a behavioral analysis program and (3) reexamination of the morphology of live, hand-collected specimens of *T. inconstans.*

Methods

We queried the MBARI archives through the MBARI software "VARS" for midwater dives with "Thalassocalycida" or any lower taxonomic nomenclature, and the same for "Euphausiacea." Data were constrained to midwater dives in which the two midwater biologists at MBARI were chief scientists, in order to avoid misidentification. The query returned 725 entries for *T. inconstans* from 1989 to 2005,

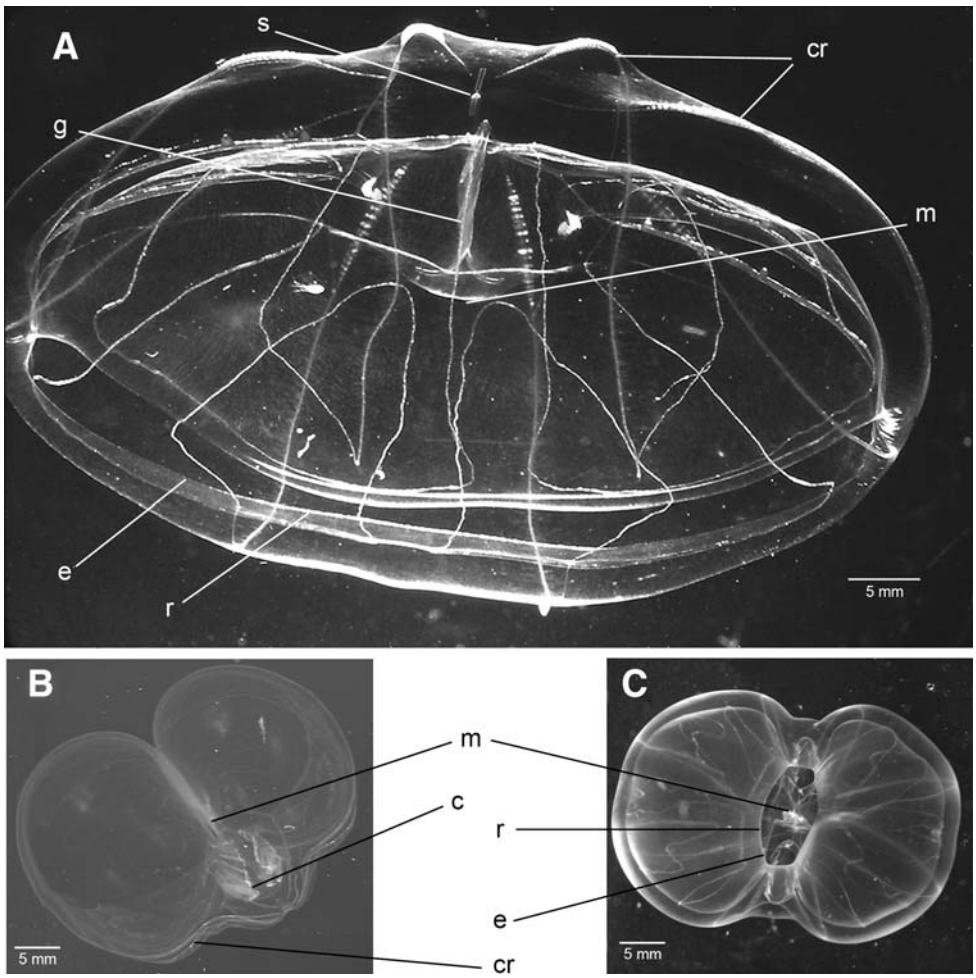

Fig. 1 **a** *Thalassocalyce inconstans* in the open "bell" form; **b** "two globe" form; **c** oral view in the "two globe" form. *c* canals, *cr* ctene rows, *e* edge of bell, *g* gut, *m* mouth, *s* statocyst, *r* ring muscle

from several locations, although only individuals from the Gulf of California and Monterey Canyon are included herein. Multiple entries for one individual were eliminated, as were sightings that did not have associated hydrographic data. After culling the data, we had video records of 288 individual *T. inconstans:* 64 from the Gulf of California and 224 from Monterey Canyon, as well as 2,437 euphausiid records: 25 from the Gulf of California and 2,412 from Monterey Canyon. Observational data were corrected for the amount of time spent at each depth bin of 50 m. CTD data for every midwater dive from 1989 to 2005 were converted into time-at-depth based on the frequency of CTD recording, giving an expected distribution if *T. inconstans* or euphausiid distribution was uniform within depth bins. Times at depth were converted into expected distributions for each location and species, and a Chi-Squared test with a Yates continuity correction was performed. Observational data were divided by time to create an encounter rate, or number of observations per minute. The data violated tests of normality, even using the usual transformations, so non-parametric statistical tests were employed. The weighted-mean depth for each species and location was calculated and a Spearman Rank test with a correction for tied ranks was used to correlate the ctenophore and euphausiid distributions in each location.

Most sightings were brief as the ROV drove by, but some lasted for several minutes. From these observations we used two video sequences for analysis of *T. inconstans* feeding behavior. The video sequence for our primary behavioral analysis was obtained from a broadcast quality, color video camera on the *ROV Tiburon*, deployed off the *R/V Western Flyer* in the Gulf of California in late March, 2003 (Robison 1992, 1999). *T. inconstans* was taped without disturbance at 250 m for about an hour. A second, 25 s video sequence of *T. inconstans* was recorded at 250 m depth over the Monterey Canyon on 29 March 2003. The behaviors observed in these clips prompted us to re-investigate the muscular control of the bell. We subsequently examined several live specimens captured by hand while blue-water diving east of Barbados in April, 2006. We videotaped bell contraction in the laboratory aboard ship in high-definition, either in small aquarium tanks or in a glass dish over a dark-field light table. Photomicrographs of the edge of the bell and circular muscle band were made with a Wild stereomicroscope equipped with a Nikon digital camera.

The Noldus Observer behavioral analysis program (Noldus Information Technology, http://www.noldus.com) was used to code the behavior and interactions of the euphausiid and the ctenophore, and to obtain temporal sequence statistics. Descriptors were either coded as Events, which were transient and lasted for only one frame (1/30 s), or as States, which lasted for an extended, identifiable duration of time. Euphausiid behavior during the five minutes prior to the start of ingestion was encoded using descriptors: "null" (State—hovers at a sixty degree angle and stays in one place, swimming neither forward or backward), "swim" (State—swims horizontally either forward or backward), "probe" (Event—slight contact with intra-globe wall by euphausiid antennae), "tail-flip" (Event—lobstering away), "contact" (Event—any euphausiid body contact with ctenophore tissue lasting one frame in duration) and "darting" (State—erratic swimming often punctuated by repeated tail flips or contact with ctenophore tissues). Lag sequential analysis was used to determine the statistical significance of various euphausiid behaviors.

Results

We plotted archived data for *T. inconstans* to assess depth distributions in Monterey Canyon and the Gulf of California. In Monterey Canyon, *T. inconstans* was found as deep as 3,512 m, although most individuals occurred above 500 m, with the 25th and 75th percentiles being 222 and 371.3 m, respectively (Fig. 2a). In the Gulf of California, however, this ctenophore was only twice found deeper than 220 m (25th = 219.75 m, 75th = 276 m) (Fig. 2b). The weighted-mean depth in Monterey Canyon was 443 m, which was deeper than in the Gulf of California at 238 m, even though both locations had the highest encounter rates between 200 and 300 m.

In the Gulf of California 65.6% of the individuals found were above or in the oxygen minimum layer (OML), in water with 0.1 ml l^{-1} [dO] or less and many were found in completely anoxic water (Fig. 2b). Although the oxygen minimum off Monterey rarely reaches anoxia, 28.9% of the specimens were in water with <1 ml l^{-1} [dO], with the lowest being 0.17 ml l^{-1}.

In Monterey Canyon various species of krill occurred down to 2,300 m (Fig. 2a); distribution of krill in the Gulf of California, however, was quite different, with a fairly sharp cut off at 400 m and with 96% of individuals found in waters with oxygen levels <0.5 ml l^{-1}, right above the oxygen minimum layer (Fig. 2b). The weighted-mean depths for euphausiids in Monterey Canyon and the Gulf of California were very similar, at 272 and 274 m, respectively (without outliers in the Gulf of California, the weighted-mean depth was 232 m).

The Chi-Squared test showed that both species in both locations had distributions that were highly different from the expected distributions ($P < 0.001$ for all). Additionally, the Spearman Rank test showed that the distribution of *T. inconstans* and euphausiids were highly correlated in both Monterey Canyon and the Gulf of California ($P < 0.0001$). The distribution of euphausiids was also correlated with the oxygen profile in the Gulf of California

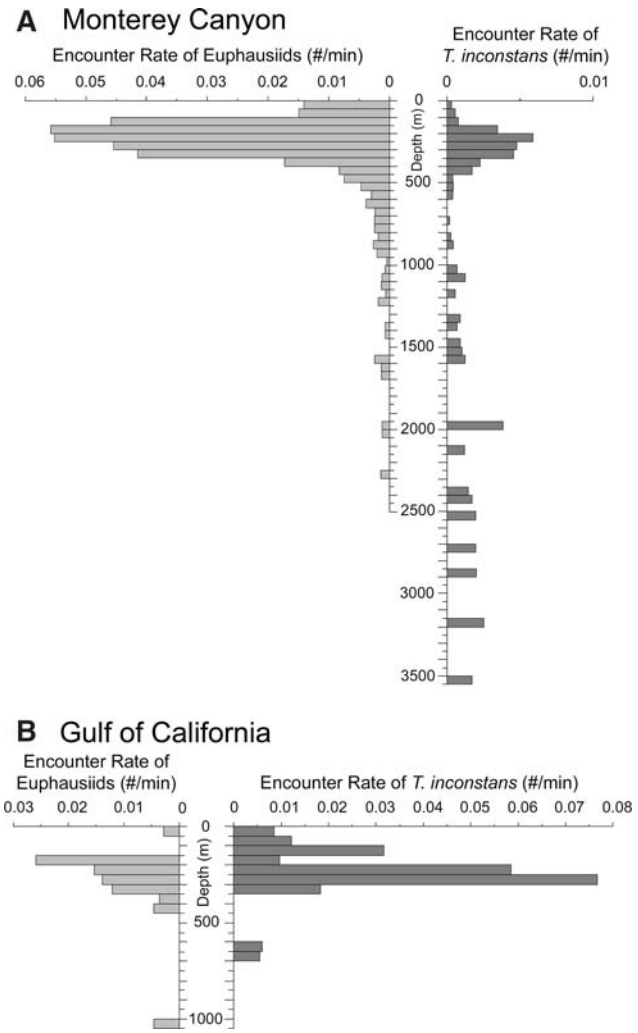

Fig. 2 Depth distribution of *Thalassocalyce inconstans* encounter rate (*right side* in *dark grey*) and euphausiids (*left side* in *light grey*) for **a** Monterey Canyon and **b** the Gulf of California. All depth distributions were significantly different from an expected uniform distribution

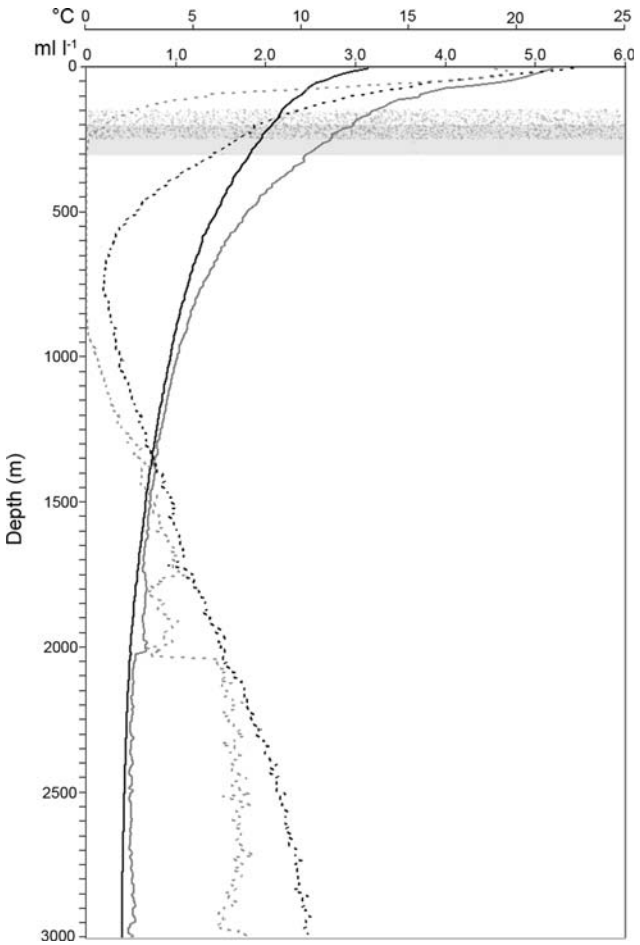

Fig. 3 Average temperature (*solid*) and oxygen (*dashed*) profiles for Monterey Canyon (*black*) and the Gulf of California (*grey*). Shading indicates 100 m with the most *Thalassocalyce inconstans* (*grey*) and euphausiids (*dotted*) and is the same for both locations

($P = 0.0224$) and Monterey Canyon ($P < 0.0001$), as well as with the temperature profile, with warm water yielding higher numbers of euphausiids ($P < 0.0001$, both locations) (Fig. 3). The occurrence of *T. inconstans* was not significantly correlated with oxygen in either location. A subset of these data, using dives in which *T. inconstans* and euphausiids were seen, showed that the weighted-mean depths were exceedingly close to the full dataset.

The 25 s video feeding sequence from Monterey Canyon showed *T. inconstans* fully extended into an almost perfectly flattened plate (Fig. 1a). Then suddenly (after an unidentified stimulus), the ctenophore rapidly contracted its bell, enclosing and entrapping a substantial volume of seawater, forming two globes (Fig. 1b, c). The two globes were pressed tightly together, sealing in the entrapped water and prey. Complete contraction of the bell occurred in slightly <0.5 s. This behavior was not only unusual but envelopment appeared to occur far too rapidly for normal ctenophore muscles, and we predicted that they probably had a peripheral ring muscle that mediated this behavior.

The observations made in April 2006 at sea off Bermuda with ctenophores in the lab aboard ship showed similar results. *T. inconstans* in the expanded hemispherical form responded to very mild stimulus from a fine needle on the inner surface of the lobe by rapidly contracting in 0.8 s into the 2-globe form, and tightly closing off the bell opening. Microscope observations confirmed the presence of a peripheral ring muscle.

The specimen of *T. inconstans* we recorded in the Gulf of California was first seen after it had already entrapped a euphausiid within its bell, but had not yet captured it in the mouth. The captured euphausiid (probably *Euphausia diomedia)* hovered upright at a 60° angle inside the globe, in contrast to the free-swimming, active euphausiids visible in the background, but the euphausiid then swam to the inside surface of the globe and lightly touched the intra-globe wall with its antenna. This behavior was repeated again and

Table 1 Observations on number, rate, and duration of behavioral States and Events in a euphausiid trapped by *T. inconstans* (Gulf of California video sequence)

	Euphausiid						*T. inconstans*	
	Swim	Null	Darting	Tail-flip	Contact	Probe	Null	Contracts
Total number	8	5	6	12	4	39	6	6
Rate (#/min)	1.4	0.9	1.1	2.2	0.7	7.0	1.1	1.1
Total duration (s)	240.5	81.5	12.0	–	–	–	309.0	25.0
Total duration (%)	72.0	24.4	3.6	–	–	–	92.5	7.5
Mean duration (s)	30.1	16.3	2.0	–	–	–	51.5	11.8
Euphausiid								
Swim	0–0	0–0	0–0	0–15	0–0	0–54	–	–
Null	0–50	0–0	0–0	0–0	0–0	0–17	–	–
Darting	33–36	0–18	0–0	17–18	17–9	0–18	–	–
Tail-flip	17–24	8–14	0–10	0–14	8–5	0–19	–	–
Contact	40–57	0–0	0–0	0–0	20–14	0–14	–	–
Probe	0–4	0–3	0–6	2–14	2–5	22–59	–	–

Second part of the table shows incidence of this behavior (%) within 1–5 s of the lefthand behavior

again, a behavior previously undescribed for any euphausiid (Hamner and Hamner 2000), which we term "probing."

The euphausiid probed 39 times in <5 min. It tail-flipped 12 times and darted 6 times for a total of 12 s, 4% of the total observation time. The euphausiid swam slowly, forward or backward, 72% of the time (Table 1). The euphausiid's only activity besides swimming within the first two and a half minutes was probing. The frequency of probing increased with time, from 0.03 to 0.1 probes s^{-1} to 0.3 probes s^{-1} each minute, then decreased slightly in the fourth minute (0.2 probes s^{-1}). Other behaviors which caused ctenophore contraction increased with time, but these had much lower frequencies. Tail-flips, the general euphausiid escape response, caused ctenophore contraction 3 times (25%). In contrast, 3 of the 5 times (60%) body contact initiated ctenophore contraction. The ctenophore did not always contract when the euphausiid darted (30%) but it did respond when darting behavior lasted several seconds. The probability of risky behavior (darting, tail-flip, contact) was low, while the probability of probing was high: 1 s after probing, the euphausiid would probably probe again (22% likelihood) with probing more likely than any other activity (0–2%; Table 1) and the likelihood of probing within 5 s after any other behavior was high (Table 1).

Discussion

The OML imposes limits for vertical daytime depth distributions of zooplankton, and although this layer can be penetrated by some species, it acts as a barrier to vertical distribution for many others (Brinton et al. 1986; Sameoto et al. 1987; Escribano et al. 2000; Vinogradov and Shushkina 2002; Giesecke and González 2004; Vinogradov et al. 2004). Almost all euphausiids encountered in the Gulf of California were concentrated between 200 and 400 m, which is also the depth range where [dO] falls below 0.1 ml l^{-1} until it reaches zero; in stark contrast, euphausiids in Monterey Canyon were found throughout the water column and [dO] never fell to these concentrations. In the Gulf of California, the euphausiids encountered by the ROV were all in <0.5 ml l^{-1} [dO], with the majority below 0.1 ml l^{-1} [dO]. Euphausiids may remain as deep as possible to avoid predators, but their ability to reach dark waters is also limited by their own oxygen requirements (De Robertis et al. 2001).

Thalassocalyce inconstans was also most abundant at 300 m; all individuals in the Gulf of California were above 700 m, despite repeated video surveys at greater depths. Most of the ctenophores in the Gulf of California were in waters depleted of oxygen (<0.15 ml l^{-1} [dO]), above the strong oxygen minimum layer between 250 and 320 m. In contrast, there is apparently no depth limitation for this species in Monterey Canyon, since *T. inconstans* was occasionally found at depths of over 3,500 m. This is further supported by the shallower weighted-mean depth for *T. inconstans* in the Gulf of California (238 m) than in Monterey Canyon (443 m). The Chi-Squared goodness-of-fit test indicated that the distributions of euphausiids and *T. inconstans* were significantly different from expected based on a uniform distribution, varying only by diving time of the ROV at depth ($P < 0.001$ in all cases) and therefore were not sampling artifacts. The high correlation between *T. inconstans* and euphausiids at each location suggests further that *T. inconstans* is concentrated where prey are most abundant, while the high correlation between euphausiids and the oxygen profile, in combination with the

weighted-mean depth being just above the OML, suggests that euphausiids avoid the lowest oxygen concentrations. Based on our knowledge of ctenophore and euphausiid physiology and behavior, this hypothesis seems the most plausible, but cannot be verified given current evidence.

It is clear that oxygen-deficient waters in the Gulf provide a barrier limiting the vertical distribution of organisms. Below the OML, oxygen levels eventually increase with depth due to lateral advection, allowing deep-living organisms to survive. However, the OML is hypoxic enough and thick enough that vertical migration is effectively diminished, as night and day distributions for zooplankton are not significantly different (Jimenez-Perez and Lara-Lara 1988). Apparently, normally vertically migrating euphausiids gather during the day at the deepest point in which they can still survive, between 200 and 400 m, where oxygen levels are very low (Fig. 3). Many gelatinous predators, including *T. inconstans,* can withstand extreme hypoxia, and they can perform as effective predators at very low oxygen levels (Decker et al. 2004; Shoji et al. 2005; Thuesen et al. 2005a, b).

Euphausiids exhibit tail-flipping escape responses to most predators, but in order to survive, euphausiids also must develop specific escape responses for specialized predators. Generic escape responses (rapid tail-flipping) may help them escape visual predators, such as penguins and fish (Kils 1979; Hamner 1984; O'Brien 1987), but generic escape behaviors may not provide protection from predators that have specialized modes of fishing, as do tentaculate medusae and ctenophores (Hamner et al. 1983; Hamner and Hamner 2000). A different suite of sequential behaviors is exhibited by euphausiids when they attempt to escape from cydippid ctenophores (for specifics, see Hamner and Hamner 2000).

The body plan of thalassocalycid predators is different from that of all other ctenophores, presenting euphausiids with a different set of predator-specific problems. *T. inconstans* encloses its prey, and the generalized euphausiid darting or tail-flipping escape behavior is then maladaptive because these behaviors will cause the euphausiid to encounter the inner walls of the bell, which are coated with sticky mucus. Accordingly, when captured by *T. inconstans*, the euphausiid initially hovers in place, a behavior which has only been recorded for euphausiids in enclosed spaces, demonstrating that the euphausiid is aware it has been trapped (Miyashita et al. 1996). It then begins to carefully search for an opening in the lobe-like folds by repeatedly probing the walls, which does not stimulate the ctenophore to contract. Probing was simultaneous with ctenophore contraction only once, when the euphausiid probed at the location of a potential exit (the seam between the two still inflated globes), after which the ctenophore pressed its lobes more tightly together, sealing both compartments. Although enclosed within the folds of the predator for five minutes, the euphausiid only darted 6 times, mostly later in the observation sequence. The euphausiid returned to probing immediately after each darting episode. All other contractions by the ctenophore were stimulated within one second of hard contact by the euphausiid with the ctenophore wall, either by contact, tail-flipping, darting, or a combination of the three.

When feeding by *T. inconstans* was initially described by Harbison et al. (1978), it was observed catching small copepods on its inner surface. It did so by floating motionless in an outstretched discoidal shape. When copepods touched the flattened surface, they adhered to the mucus coating, and were subsequently transported to the mouth via cilia on the ctenophore's inner surface. In this process *T. inconstans* never contracted from the fully expanded discoidal shape, acting like a "passive trap" (Harbison et al. 1978). This feeding mechanism, however, cannot explain how larger and faster prey, like euphausiids, could be captured.

Thalassocalyce inconstans can contract within 0.466 s in response to external stimuli, explaining how free-swimming euphausiids are captured by the feeding disc. The rapid contraction of the bell changes its shape from an open, flat configuration to a sphere, enclosing a volume of water and prey like a purse seine around a school of fish. From this, the configuration slowly changes to resemble the two lobes of a lobate ctenophore. The biradial globes press together, and slow contractions of the bell expel water while remaining sufficiently closed to prevent escape of the prey.

Our video sequences showed that *T. inconstans* could close its lobes in less than half a second, and it was clear that the musculature of the lobes of the order Thalassocalycida needed to be re-examined since no unusual muscles had been described previously for the feeding disc. We postulated that such rapid closure could be effected best via a circumferential sphincter or ring muscle. One of us (LM) subsequently examined two specimens of freshly captured *T. inconstans* and confirmed that there is indeed a relatively large ring muscle around the outermost edge of the ctenophore lobes (Fig. 1). When this muscle contracts it draws the lobes of the ctenophore closed like a purse string. *T. inconstans* has thin, flaccid tissues, which stretch to envelop a large volume of water when the ring muscle contracts, thus producing the two-globed compartment. No previous record of this type of muscle or feeding mechanism has been recorded in Ctenophora, but entrapment of water and prey prior to ingestion has been observed for the scyphomedusa *Deepstaria* sp. (Larson et al. 1988), the mollusc *Melibe leonina* (Hurst 1968), an anemone, *Amplexidiscus fenestrafer* (Hamner and Dunn 1980), the squid *Grimpoteuthis* sp. (Hunt 1999), and is analogous to the feeding behavior of pelicans and baleen whales. A similar

adaptation can be seen in the carnivorous doliolid, *Pseudusa bostigrinus* (Robison et al. 2005a). This muscle band makes it possible for *T. inconstans,* a slow swimmer, to contract rapidly enough to capture relatively large, rapidly swimming euphausiids.

The rapid closure of the bell may also help explain why the peculiar morphology of Thalassocalycida evolved. Gelatinous species have a greater diversity of different muscle fibers than land animals (Bone 2005). Although typical in hydromedusae, ring muscles are not known in other orders of ctenophores. Lobate ctenophores have muscular lobes, but they are unlike the muscle discovered in Thalassocalycida (Bilbaut et al. 1988; Tamm and Tamm 1989; Seipel and Schmid 2005). This remarkable adaptation allowed thalassocalycids to evolve a much different body plan from ctenophores in the Order Lobata, one that permits it to quickly engulf relatively large volumes of water and capture fast prey. Initially, only the ring muscle contracts, so that the ctenophore encloses both prey and seawater surrounding it. Subsequent contractions of the bell along the tentacular plane divide the globe into two connected compartments that are closed to the outside. Thus the euphausiid in our observation sequence was able to swim freely from one hemisphere into the other. Eventually the opening between the two spheres closed fully, and the two globes contracted somewhat independently. This body plan and behavior enable thalassocalycids to initially trap prey by closing off all openings quickly, and thereafter to separate the prey from the entrapped seawater.

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